MERA food web assembly: when predation tends to be specialized

Jade, June 12

The main problem of the previous MERA-based food web assembly procedure is the assumption that all species between two adjacent trophic levels are connected. In this write up, an extra parameter γ quantifying the cost of preying on more functional diversity (more species or species with higher D_r) is included. When $\gamma = 0$, there is no cost for having more prey species, as was assumed in the previous framework. The bigger the γ, the more it costs for the predator to feed on an extra prey species.

1 The cost to be a generalist

γ quantifies the cost in efficiency for the predator to catch prey with more functional variation, a positive value for γ meaning that the higher the functional variation in prey, the harder it is for the predator to catch them. Capture efficiency is annotated by τ_c, in contrast to the utilization efficiency τ_u (the τ that has been used in previous MERA-based food web assembly procedures). τ_c can be different for each species (annotated with $\tau_{c,i}$ for

species i) and is calculated as following:

$$\tau_{c,i} = e^{-\gamma \sum_p^{P_i} D_{r,p}} \tag{1}$$

$D_{r,p}$ is the relative individual distinguishability for the p_{th} prey of species i (in total P_i prey species). Eq. 1 is derived from a simple way to formularize γ based on its definition:

$$\gamma = -\frac{d\tau_c}{\tau_c dV_p} \tag{2}$$

V_p is the total functional variation in prey and is proxied by $\sum_p^{P_i} D_{r,p}$ (this is because we interpret D_r as $D_{within}/D_{between}$, the former is functional variation within the species and the latter is that between any two different species which is assumed to be a constant here). From Eq. 1 we can see that, when adding a new prey, τ_c has to decrease as long as the D_r of the prey is not zero.

To clarify the difference between capture efficiency τ_c and the utilization efficiency τ_u, first, the former is the proportion of the steady state prey supply that is captured by the predator, while the latter is the proportion of prey captured that is transformed into predator biomass. Second, τ_c is species specific and decreases with the functional diversity of prey, while τ_u is a universal parameter for all species indicating a biophysical constraint on transferring food to body mass. Third, τ_u only affects the steady state abundance of the predator but not that of the prey, in other words, the proportion of captured prey mass not transformed into predator body mass

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$(1 - \tau_u)$ is lost eternally from the food web as heat. In contrast, τ_c does not only affects the predator abundance but also affects prey abundances because the proportion of prey not captured $(1 - \tau_c)$ still exists in the food web and should be included when calculating the steady state abundances for preys.

With the clarifications above, next I will illustrate how τ_c and τ_u each is incorporated into the existing MERA framework. First for τ_c: when calculating the steady state abundance of a predator species, its resource requirement θ is divided by τ_c to calculate the capture-adjusted resource requirement $\theta_c = \theta/\tau_c$, or the amount of resource needed for θ units of resource to be actually captured so that one predator individual is maintained. It is then the θ_cs of the competing species that are effectively used in MERA equations calculating their steady state abundances. In this way, predators with higher τ_c (those that prey on less functional diversity, or specialists) are given a competitive advantage compared to those with lower τ_c (those that prey on higher functional diversity, or generalists) by having a lower effective resource requirement. After steady state abundances are calculated for all predators, preys not captured are added back to their steady state populations. For τ_u, it is much simpler: the abundance of prey (or total energy content $\theta \times N$) is multiplied by τ_u before using it as the resource for predator species.

With τ_c and τ_u incorporated, the MERA-based food web can be

assembled from the same logic as before: species invade the community sequentially and each new species settles in the trophic position that gives it the highest steady state abundance.

2 Finding the optimal set of prey

In this new model, there is one additional decision each species has to make when settling into a trophic level higher than the basal: which of the species at the lower level to prey on (to achieve the highest steady state abundance). Notice that since there is a cost in capture efficiency by including more prey species (γ), the optimal set of prey is not necessarily all species at the lower level but a subset of it. Below is a description of the algorithm to find the optimal set of prey:

When finding the optimal prey set for the new species to be at trophic level $i > 1$, initially all species in trophic level $i - 1$ are on the candidate list.

1) Calculate the steady state abundance of the new species taking each species on the candidate list as the single prey for it. If the species has no other predators, the new species simply takes half of its steady state abundance. If there are other predators existing, the new species has to compete with all of them.

2) Add the species with the highest value to the prey list and remove it from the candidate list.

3) Update the τ_c of the new species with the D_rs of species on the prey list using Eq. 1.

4) Repeat 1-3 until adding one more prey species does not increase the steady state abundance of the new species.

After calculating the optimal steady state abundance for the new species as above for all available trophic levels, if the highest value is bigger than the minimum viable population size e, invasion is successful and the species will be added to the trophic level corresponding to the highest steady state abundance. Otherwise invasion fails and the species will not be added. Notice that in this new model, entry of a new species potentially affects all other species, whether they are in a lower (through the prey selection process), higher or the same trophic level as the new species. In other words, there is not only bottom-up but also a top-down effect. Therefore after adding one species, the abundances of all species in the food web have to be recalculated. With $e > 0$, it is possible for the invasion of a new species to trigger extinction cascade for multiple species or even a whole trophic level.

The new algorithm takes much longer time to run because of the additional prey selection process and a higher chance of extinction cascade due to the addition of a top-down effect. Results from some first trials are shown in the next section.

3 Result

In all following graphs, species are represented by circles (size is proportional to θ) on horizontal dotted lines representing trophic levels. The energy flows between species are represented by arrows, the width of which is proportional to the magnitude of the energy flow.

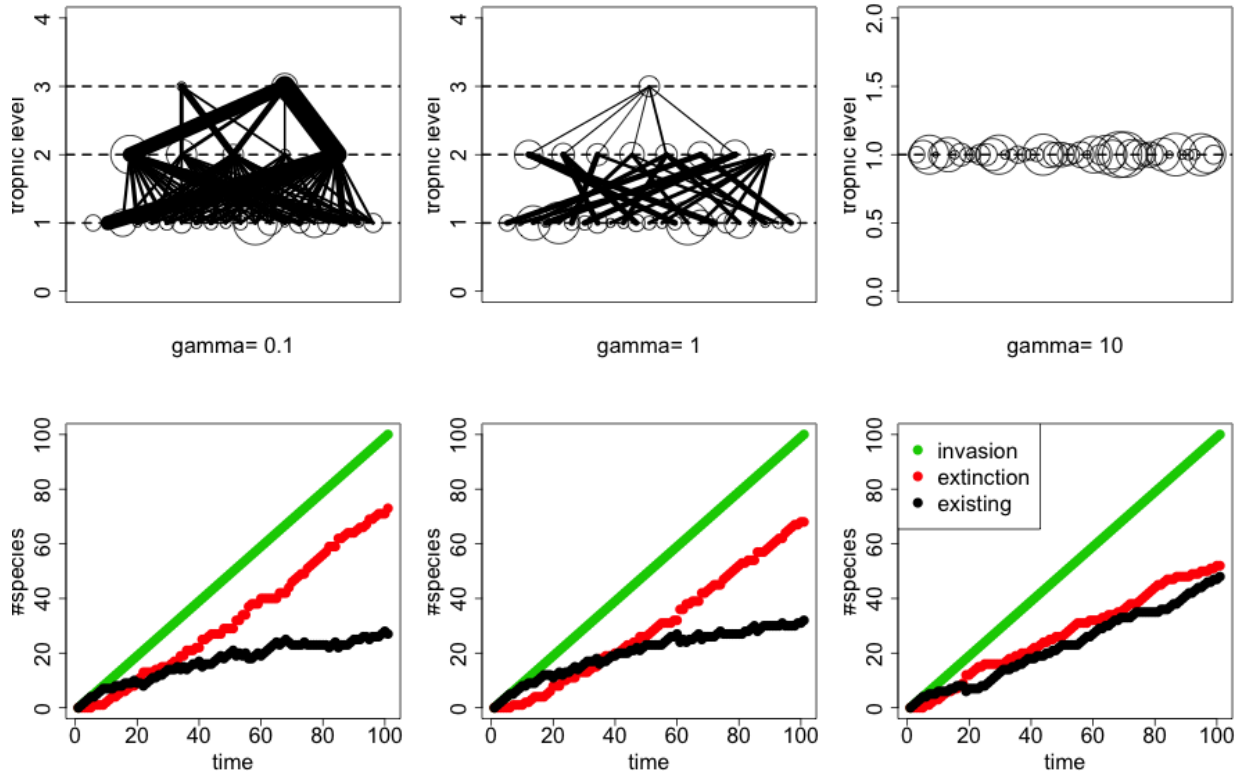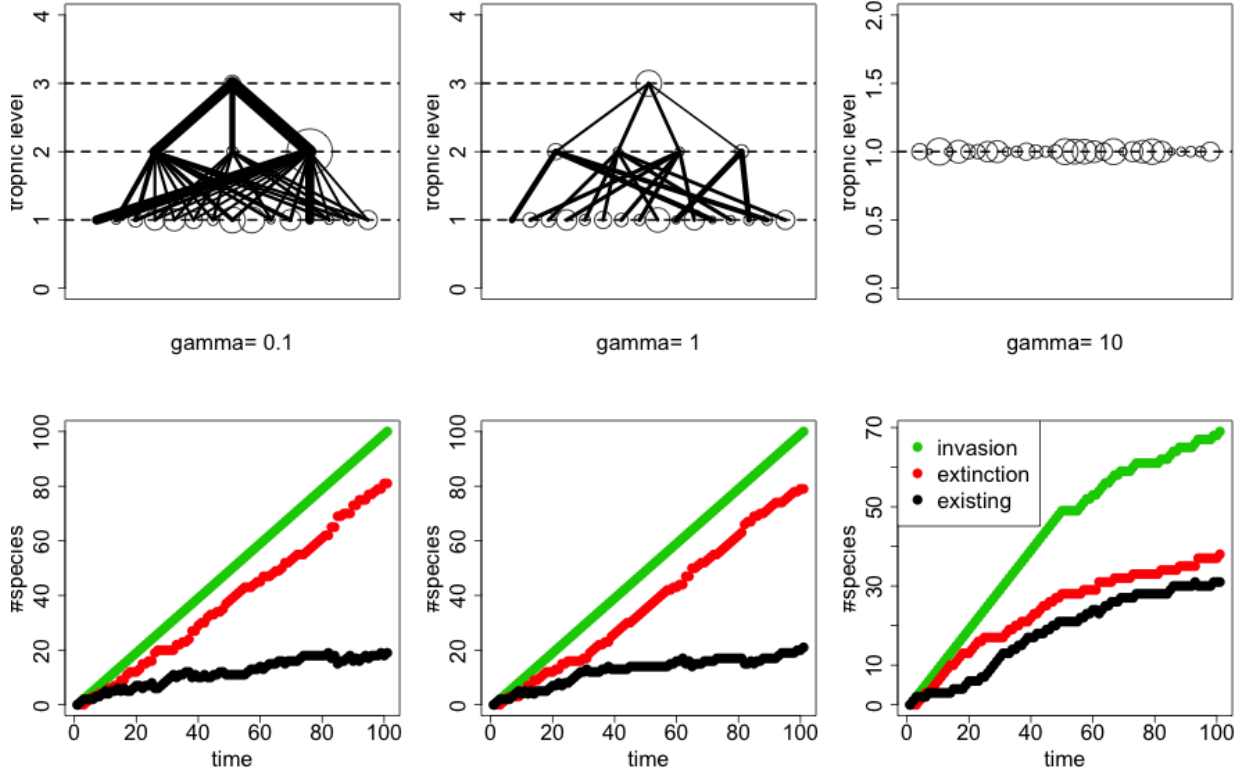## 3.1 γ effect (when $D_r = 0.1$)

Fig. 1 Food web structure with γ when $R = 50e\mu$

Fig. 2 Food web structure with γ when $R = 20e\mu$

As γ increases, species become less connected to each other, indicated by the fewer number of trophic links and the thinner energy flow between trophic levels. This of course makes sense because γ quantifies the cost in capture efficiency to feed on more diverse prey and therefore the bigger the γ, the less beneficial for a species to be a generalist predator and fewer trophic links there are in the food web. Also the number of species increases with γ, possibly a side effect of the less connectedness of the food web (less energy loss through τ_u and more energy retained in the food web, potentially supporting more species)

γ is not the only factor that affects the connectedness of the food web. In the following we will see that D_r also has an significant effect.

3.2 D_r effect (when $\gamma = 1$)

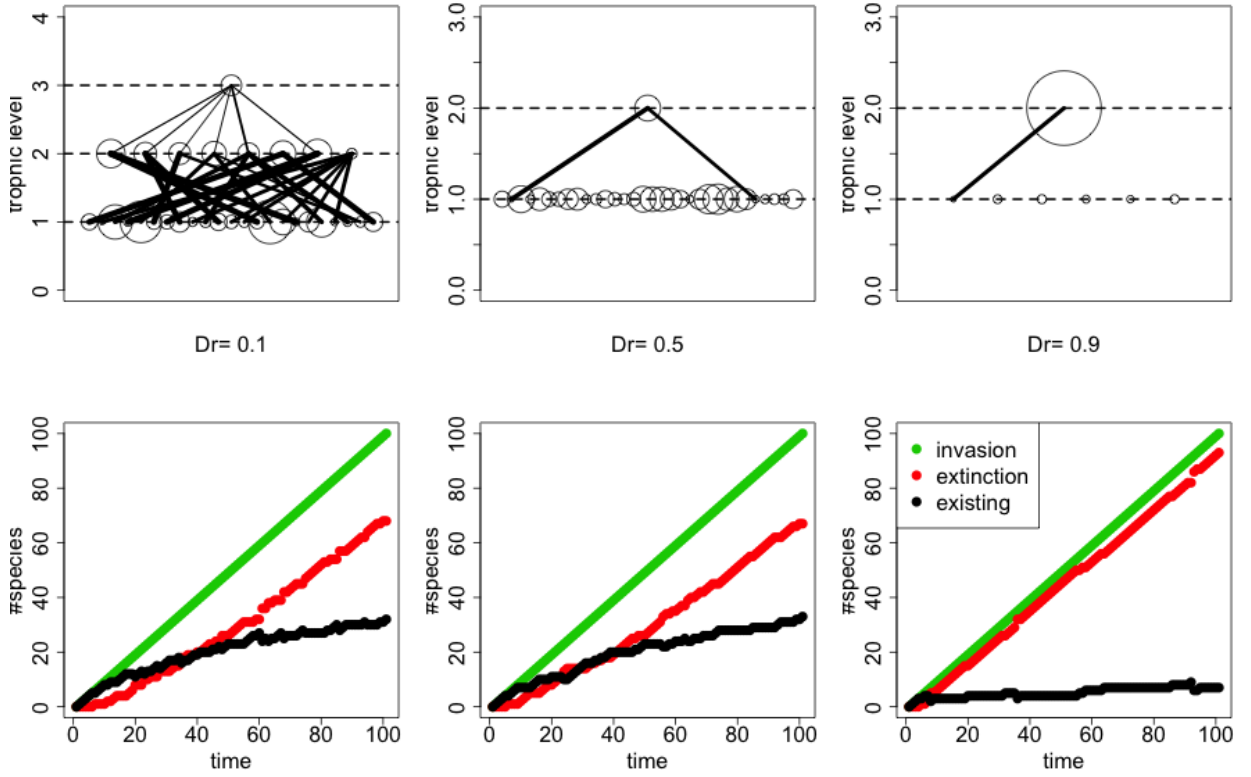In the caption, μ is the mean θ of the species pool.

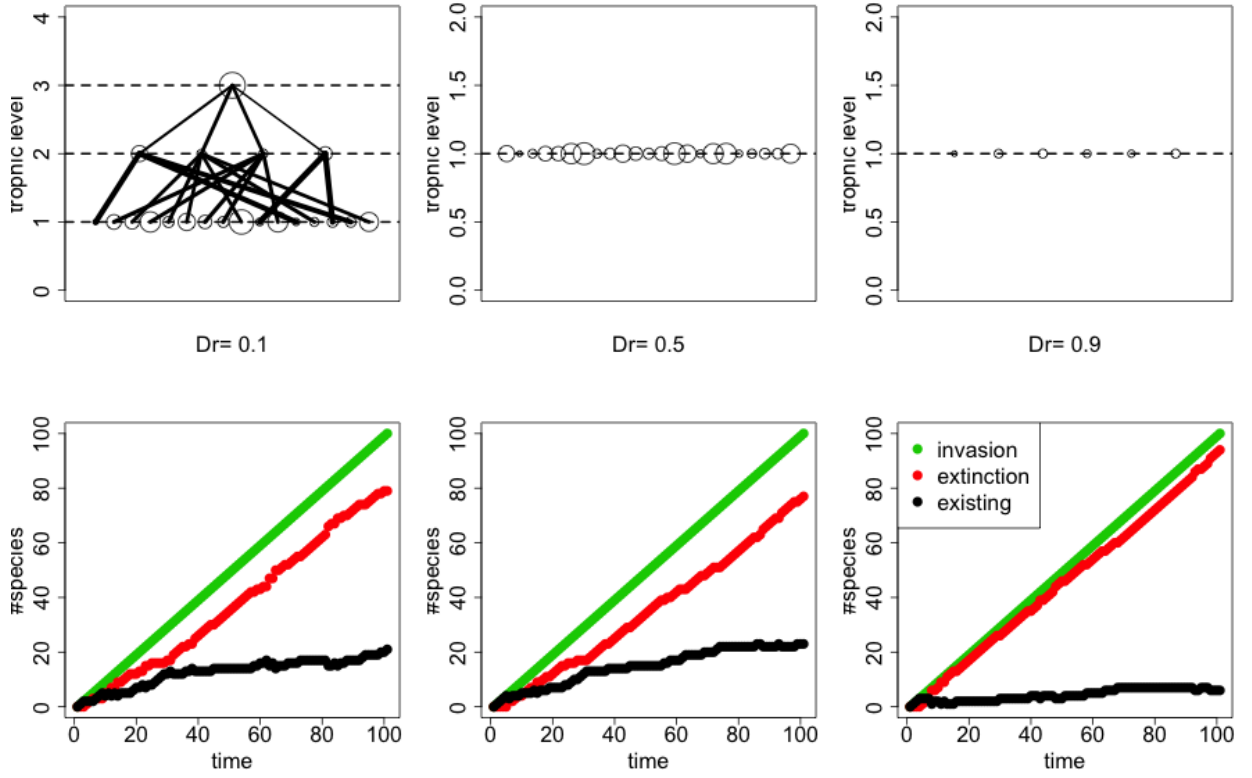
Fig. 3 Food web structure with D_r when $R = 50e\mu$

Fig. 4 Food web structure with D_r when $R = 20e\mu$

From the graph we can see that the higher the D_r, the less connected the food web becomes, just as with a bigger γ. However, the number of species is lower for a higher D_r, probably due to the increased competitiveness (less chance of coexistence) among species.

Unlike in the previous version where complete connectedness between adjacent trophic levels is assumed, in this new model, the extent to which species are connected through trophic links is significantly affected by D_r. Especially when comparing $D_r = 0.1$ and $D_r = 0.5$, the number of species is not much different between these two scenarios, but the number of trophic

links and the amount of energy flow are both significantly higher for
$D_r = 0.1$.

Based on this new model we can do analysis on all metrics of the food web and see what γ and D_r values give a structure that most resembles what is observed in nature. In the next section, the link-species relationship emerging from this procedure will be shown.

4 Link-species relationship

Using the procedure above, food web structure is simulated for a series of communities with acsending fundamental resources. For each community the number of trophic links and species eventually included are calculated. Different combinations of γ, D_r and τ_u are compared. Notice that in Martinez 1991, a species has to have at least one link with another (so the minimum number of links $L_{min} = S - 1$ instead of 0). In our model, this is equivalent to taking the fundamental resource as a species (the basal species), which is what will be done to make results comparable.

In the following figures, the link species relationship is compared among different γ (curves with different colors within the same graph), τ_u (graphs within the same figure), D_r (figures). For each specific (γ, τ_u, D_r) combination, the link species relationship is fitted to $L = aS^2$ and the value of a shown in each graph. The empirical constant connectance ($L \approx 0.1S^2$)

and the lower limit of the link species relationship $(L = S - 1)$ are also plotted in the graphs for reference.
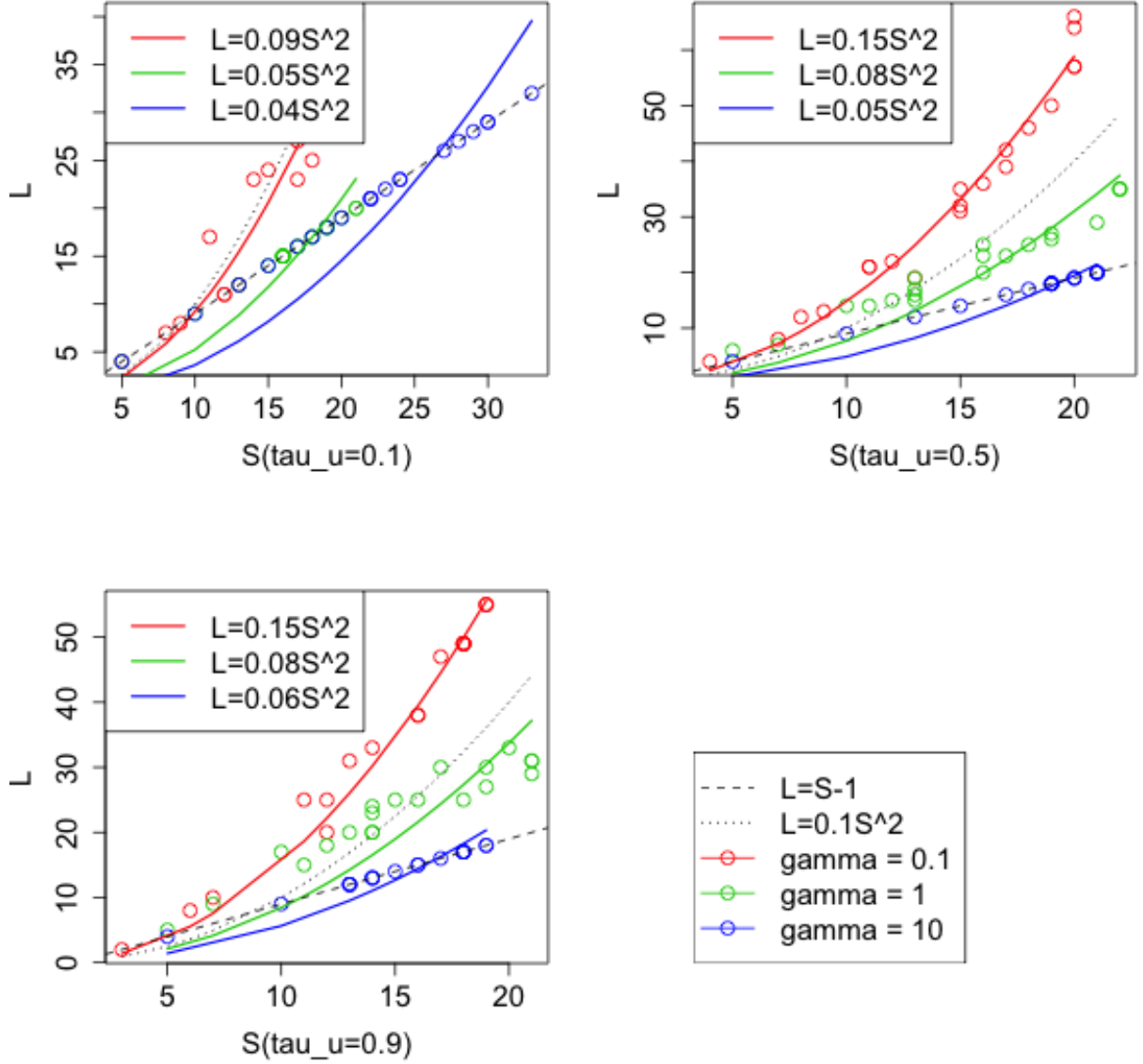

Fig. 5 Link species relationship with different switching cost (γ) when
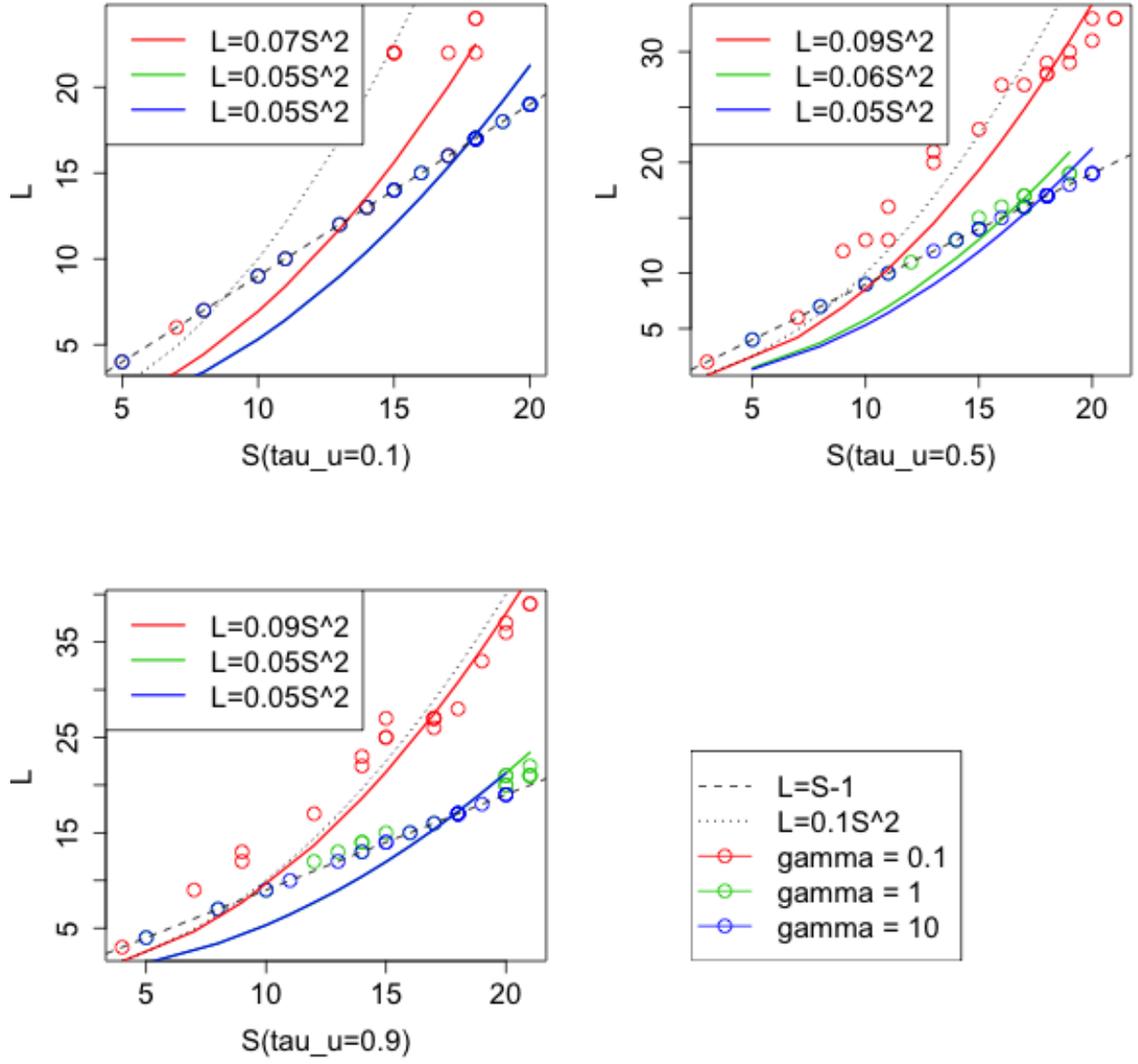
$$D_r = 0.1$$

Fig. 6 Link species relationship with different switching cost (γ) when

$$D_r = 0.5$$

In general, the bigger the γ, the slower L increases with S, which is consistent with the previous result that a higher γ undermines the connectedness of the food web by imposing a higher cost in capture

efficiency for one species to prey on multiple species. Secondly, the bigger the τ_u, all else equal, the steeper the link species relationship. One inference from this result is that ecosystems where trophic efficiency is higher (e.g. marine ecosystems) are better connected trophically. (I think I have seen a study reporting similar observations but I cannot find it any more. It seems to be about interspecific interactions being more negative/positive for terrestrial ecosystems. Any clue?) Finally, the bigger the D_r, the slower the link species relationship. In other words, there tends to be more trophic links when species are more specialized (smaller D_r).

We can see that all parameter combinations predict a very constrained range of a (from 0.04 to 0.15), adding to the difficulty of differentiating one scenario from another with limited data. Despite of this, if we take the constant connectance relationship that Neo found ($a = 0.1$) to be accurately describing data, the result here indicates that the combinations of $\gamma = 0.1$, $\tau_u = 0.1$, $D_r = 0.1$ and $\gamma = 0.1$, $\tau_u = 0.9$, $D_r = 0.5$ give patterns that most resembles the empirical pattern. Although both support a small γ, the implication for τ_u and D_r differs between the two. According to the ten percent law of Lindemann, it is more likely that τ_u is 0.1 than 0.9, which means that D_r is more likely to be 0.1 than 0.5.

Due to computational limits, here I am only showing some preliminary results that can be obtained within a day or two. To further verify the inferences, in the future more tests with wider range for all the parameters

should be done. More food web metrics could be calculated and compared with empirical observations, from which hypotheses on the effects of the parameters (community trophic efficiency τ_u, predation efficiency γ and within species variation D_r) on food web structure can be developed and tested.